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TWO TRIASSIC BRYOPHYTES FROM SOUTH
AFRICA

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(With Plate I)

ABSTRACT

Two bryophytes from the Molteno Series in Natal are considered. The first, *Hepaticites cyathodoides* sp. nov., is a thalloid liverwort, known sterile only, but showing a close resemblance in thallus structure to the living genus *Cyathodium*. The second, *Muscites guescelini* sp. nov., proves to be a moss; one of the very few mosses from pre-Tertiary rocks. Though sterile *M. guescelini* shows enough detail for a comparison with the Leucodontaceae to be suggested. Some general discussion is offered, with particular reference to the possibility that some sterile fossils may be related to living genera, and to the methods of leaf segmentation in the Bryophyta.

INTRODUCTION

Fossil bryophytes are not common at any geological horizon, and from those Triassic floras characterised by an abundance of the forking leaves of *Dicroidium* only two fossils that may be bryophytes have been recorded. There are only two major records of mosses from pre-Tertiary rocks.

Though both species described here are sterile, enough information is available to allow of close comparison with the gametophytes of living forms. The structures affording this information are readily demonstrated

by means of the balsam transfer technique. This technique, as the works of Walton, Harris and Lundblad show, has proved essential for critical work on fossil bryophytes.

The material, except for one specimen, comes from the Waterfall locality, Burnera, in Upper Umkomaas, Natal. This locality almost certainly falls within the Molteno Series, and so is of Middle Triassic age (see Haughton 1954, Townrow 1957); but the Molteno in Natal is attenuated and the exact horizon of the Waterfall locality is uncertain.

All Type and figured specimens are contained in the collections of the South African Museum, Cape Town.

HEPATICEAE

Hepaticites cyathodoides

Liverworts are delicate organisms, and even when, like the present specimens, they are very well preserved as fossils, often show some features only obscurely. I have therefore made two basic assumptions. The first is that the thallus was not originally more complicated than it now appears to be. The second is that the darker lines seen on the wing (lamina) of the thallus represent a system of partitions within the thallus separating air chambers. For shortness I propose to refer to these air chamber partitions as *internal ribs*.

The internal ribs show more than two cell layers in them, but the thallus wing elsewhere shows two only. Had there been more than two cell layers in the thallus, or other complicating structure, it seems highly probable that traces would have remained; just as more than two cell layers are visible in the internal ribs.

The evidence that the internal ribs are partitions is examined in what follows and their nature is a fundamental point in the comparison of the present material. In order to facilitate such comparisons, I have examined herbarium material of *Cyathodium cavernarum* (the Type species), *C. aureonitens* and *C. tuberosum*.

Hepaticites cyathodoides sp. nov.

(Plate I A, B; Figs. 1A—J, 2A)

DIAGNOSIS: Plant thalloid, dichotomising about every 4 mm., thallus lobes diverging at 60°—90°, apex notched. Thallus margin not waved. Midrib conspicuous, projecting ventrally, about 0.75 mm. wide, extending almost to apices. Thallus wings two cells thick, cells in rows, arching from midrib at about 30°, meeting margin at nearly 90°. Air chambers

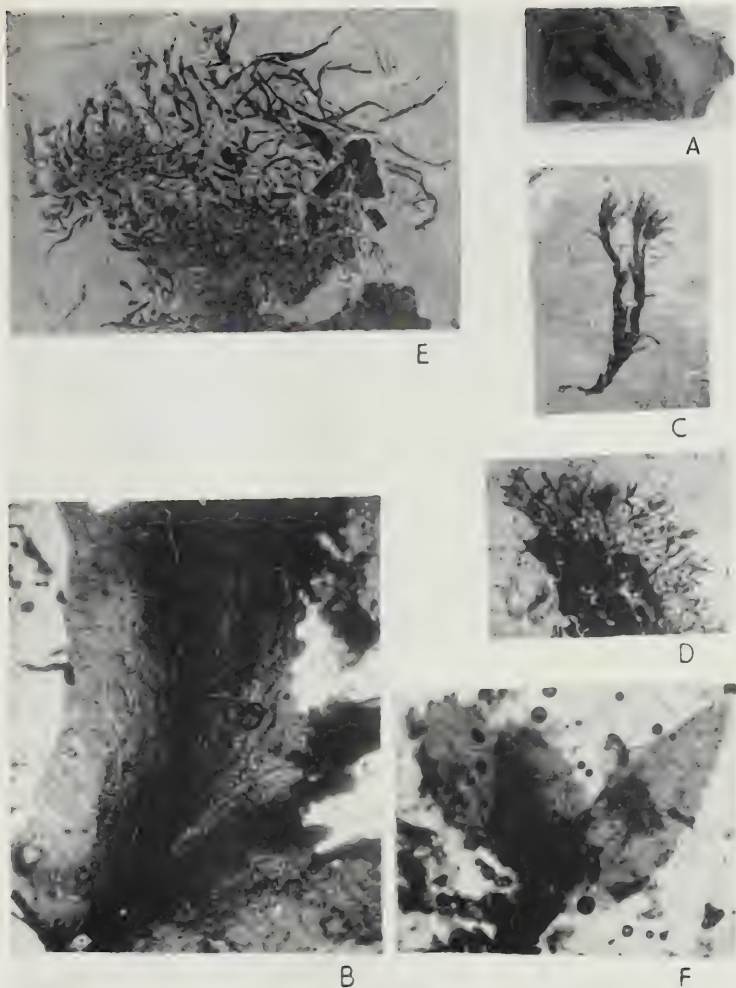


PLATE I. *Hepaticites cyathoides*, A, B; *Muscites guescelini*, C-F.

- A. The Type specimen before transferring. $\times 1.75$.
- B. Part of the thallus showing midrib and arrangement of the internal ribs. $\times 12$.
- C. The Type specimen. $\times 3$.
- D. Specimen showing a number of leafy shoots associated with a twig. $\times 1.5$.
- E. Specimens showing both leafless stems and leafy shoots. The moss is associated with debris, mostly leaf material. $\times 2$.
- F. Parts of three leaves to show the arrangement of the cells. $\times 18$.

irregular, more conspicuous basiscopically; internal ribs curving out from midrib at about 30° , arching to nearly 90° . Ribs anastomosing mainly near margin, about 0.5 mm. apart. On thallus wing ventral cells slightly elongated, oblong, $43 \mu \times 24 \mu$ (variation $20 \mu - 12 \mu$), on dorsal surface similar but smaller. Cells over midrib tending toward rectangular, $45 \mu \times 20 \mu$. Rhizoids occurring basiscopically under midrib only, but toward apices occurring also away from midrib; minimum length $120 \mu \times 8 \mu$, simple, maximum density seen, 13/mm. of thallus length. Pores on dorsal surface about 50μ across, normally nearly round, surrounded by one or two rows of small cells. Ventral scales minute, only present at apex, one cell high, 5—10 cells wide, forming one row across the midrib.

DESCRIPTION: The material consists of six small but very well preserved specimens, the largest (Plate IA) being designated the Type. Five are from the Waterfall locality, the sixth, which is identified with the Waterfall fossils, comes from the Australian Middle Triassic from the Brookvale plant bed (near Sydney). At the Waterfall all except one of the specimens occurred in rock devoid of other plant fossils; while the habit of the Type, and the fact that all the specimens were exposed dorsal side uppermost on splitting the rock (this was determined from the position of the rhizoids in transfer preparations) suggests that they may be preserved in the position of growth. The plant may have had a rosette habit.

The midrib showed on the dorsal side as an indistinct furrow, but I do not know whether it formed a furrow dorsally in life. On the ventral side the midrib always projected conspicuously.

The cellular structure was readily seen (Plate IB, Fig. 2A). The ventral cells were visible over nearly the whole thallus including the midrib, but were apparently rotted away in a few places. The dorsal cells were less distinct, being best seen where the ventral cells had rotted away and were never visible over the midrib.

The rhizoids (Figs. 1F, G, H) showed no signs of tubercles, cross walls or branching, but there was a suggestion that there may be two sorts, thick-walled and thin-walled rhizoids. The preservation does not allow certainty on this. It is also uncertain whether one sort of rhizoid was confined to one part of the thallus. The great majority of the rhizoids were broken off short, so that their maximum length is uncertain. The minimum length is obtained from a few small complete rhizoids (possibly immature) found at the apices, but the longest broken fragment was 240μ long.

The internal ribs are shown in Plate IB and Fig. 1C. Before transfer in two specimens they appeared as very slight trenches on the dorsal side of the thallus, while in the other specimens they were not visible dorsally

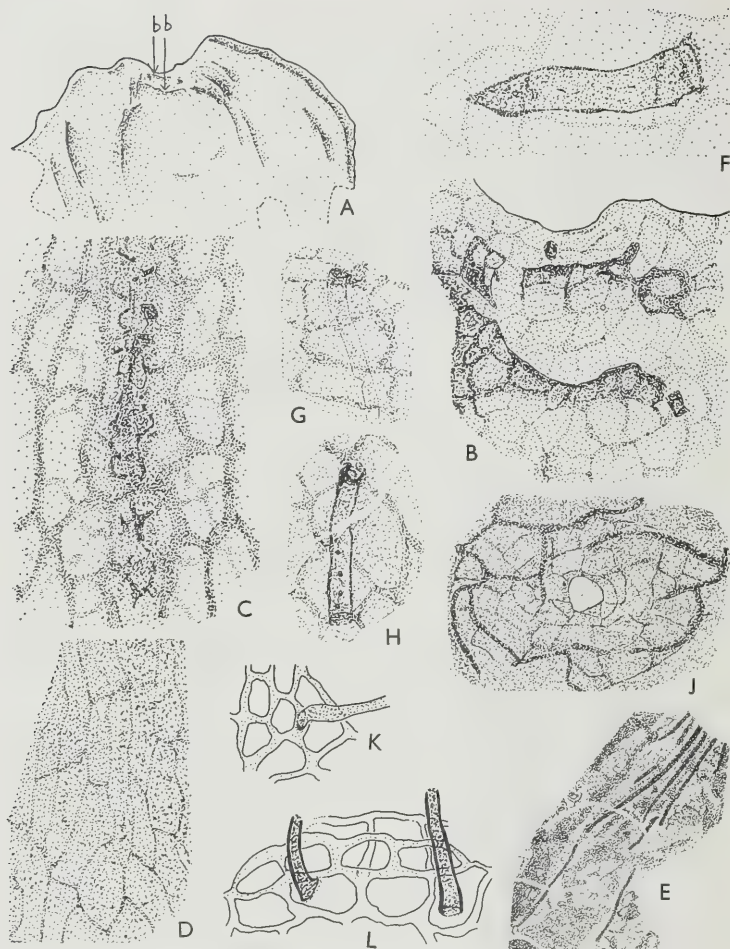


FIG. 1. *Hepaticites cyathodoides*, A-J; *Cyathodium tuberosum*, K, L.

- A. Apex of a thallus-lobe, showing ventral scales (b . . . b) and longitudinal foldings. $\times 33$. From the Type specimen.
 B. The thallus-lobe apex shown in Fig. 1A., at greater magnification, showing ventral scales, and arrangement of ventral cell rows. $\times 262$.
 C. Cells of the thallus over an internal rib, showing two cell layers only away from the rib, but indications of more than two cell layers over the rib. $\times 475$.
 D. Cells over part of the thallus midrib. $\times 144$.
 E. A group of rhizoids over part of the thallus midrib. $\times 10$.
 F. A small complete rhizoid, showing point of attachment to a cell. $\times 262$.
 G, H. A thin-walled and a thick-walled rhizoid respectively. Each rhizoid is attached basally to a cell, but is broken off short. $\times 144$.
 J. A dorsal pore, and the cells around it. The heavier lines represent outlines of ventral cells, here mostly rotted away. $\times 262$.
 K, L. The basal parts of a thin-walled and two thick-walled rhizoids respectively; L. also showing a ventral scale of abnormal form being only one cell high. (Ventral scale stippled). $\times 160$.

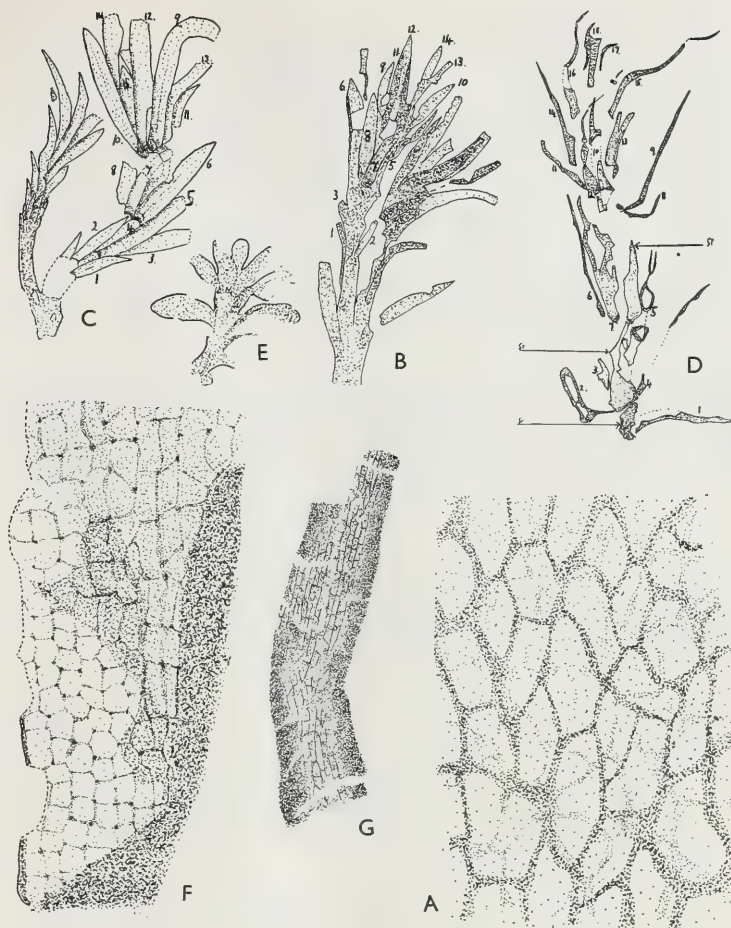


FIG. 2. *Hepaticites cyathodoides*, A; *Muscites guescelini*, B-G.

- A. Part of the thallus away from the midrib, showing two cell layers. $\times 262$.
 B, C. Apices of two shoots, showing apical tuft of leaves, and numbers suggesting the phyllotaxis. Both apices compressed parallel with one bedding plane. $\times 14$. B. from the Type specimen.
 D. A shoot compressed so that it traverses several bedding planes, with numbers suggesting the phyllotaxis. Portions marked *St.* interpreted as part of the stem. $\times 16$.
 E. A shoot apex showing leaves oblong rather than lanceolate. $\times 14$.
 F. A leaf base showing the wide margin of square or hexagonal cells of thin substance, and central, elongated cells of thicker substance. The heavy stippling represents part of a (?) stem lying partly over the leaf base. $\times 176$.
 G. Part of a stem showing epidermal cells, and thicker substance at the edges of the stem. $\times 25$.

at all. On transfer they always appeared as dark lines, similar to, but smaller than, the midrib. The internal ribs did project very slightly on the ventral surface, but the ventral cells crossed them with, at the most, only very slight distortion (Fig. 1C) and there was no sign of plates or lamellae ventrally. It may be, indeed, that the slight projection ventrally is merely the result of compression. An internal rib was always composed of at least one other cell layer in addition to the dorsal and ventral epidermes, and probably more than one extra cell layer was present.

The objects interpreted as dorsal pores (Fig. 1J) were clearest in two specimens which, for some reason, had paler substance than the others. The form of the pores was not distinct, but they always appeared about at the centre of an air chamber, and I saw many of them all consistent with one another.

The ventral scales (Figs. 1A, B) were seen at four apices and there were never more than two reasonably complete ones at any apex, indeed, basiscopically, their (presumed) position is marked only by slight irregularities on the surface of the ventral cells and at the wider (? older) apices the scales were less complete than those figured. I could discover nothing about the form of the apical cell(s), but the form of the cell rows at an apex (Fig. 1B) suggests that it cut off cells on two sides only.

In all the specimens there were fairly prominent folds, especially over the midrib, and also flanking the apices, and sometimes at the margin. These folds were irregular in size and form and are not cellular structures. I suppose they may be connected with the process of fossilization.

DISCUSSION: (a) *The nature of the internal ribs.* There are, I suggest, three possibilities here:

- (i) That they are a system of dorsal plates as are seen, for example, in species of *Riccia* and *Dumortiera* (see Coker 1903, Cavers 1911, Goebel 1930) or in *Petalophyllum* (see Mehra & Vashishti 1950, Mehra 1957);
- (ii) that they are a system of ventral plates seen, for example, in some species of *Riccardia*, e.g. *R. fuegiensis* (see Goebel 1930);
- (iii) that they are internal, some sort of partition within the thallus.

The first possibility is ruled out as, where visible at all dorsally, the internal ribs appear as furrows, not as upstanding structures. The second possibility can also be dismissed, for there is no sign of plates or cell rows over an internal rib, the whole ventral cell layer is undisturbed except, rarely, for a slight distortion of the cells. This means the internal ribs must be internal.

There are two further lines of evidence as to their nature. First, the pores on the dorsal surface, and their position roughly midway between

the internal ribs, strongly suggests a system of air chambers in the thallus. Secondly, the general form and disposition of the internal ribs closely resembles the general form and disposition of the partitions separating air chambers within the thallus of living Liverworts.

(b) *Comparisons of H. cyathodoides with living Liverworts.* The discoverable characters of *H. cyathodoides* indicate a surprisingly close resemblance to *Cyathodium*, and I am indebted to Dr. G. K. Berrie for first suggesting this similarity to me (selected references: Leitgeb 1881, Lang 1905, Khanna 1926, 1927, 1927a, Kashyap 1932, Chavan 1937, Schiffner 1924, 1938, 1939). The essential feature of the thallus of *Cyathodium* that sets it aside from other Liverwort genera is that the thallus consists only of a dorsal and ventral epidermis, separated by a system of air chambers that are bounded and separated by partitions, and that open dorsally by simple pores. As interpreted, *H. cyathodoides* has just this construction. Nearly all the other structures seen in *H. cyathodoides* can be matched in some species or other of *Cyathodium*, as is set out below.

<i>H. cyathodoides</i>	<i>Cyathodium</i>
(1) Thallus often forked, possibly of rosette habit	<i>C. griffithsii</i> of rosette habit (other species less forked)
(2) Midrib conspicuous	Midrib conspicuous in <i>C. foetidissimum</i> (inconspicuous or absent in other species)
(3) Air chambers irregular, better seen basiscopically	Air chambers irregular and better developed basiscopically in <i>C. cavernarum</i> (air chambers more or less regular in other species)
(4) Rhizoids not tuberculate, possibly thick walled and thin walled	Rhizoids never tuberculate, thick walled and thin walled; distinction rather obscure in <i>C. cavernarum</i> (plain in other species)
(5) Cells over midrib elongated, nearly rectangular	Cells over midrib elongated, nearly rectangular in <i>C. tuberosum</i> (less distinct from cells of wing in other species)
(6) Ventral scales minute, one cell high, 5-10 cells wide	Ventral scales always small, sometimes one cell high and up to 5 cells wide in <i>C. tuberosum</i> (form otherwise in other species)
(7) Ventral scales forming a single row over midrib	Ventral scales forming a single row over midrib apically in <i>C. foetidissimum</i> (in other species normally forming two rows).

There are differences; all, however, except one—the form of the dorsal pores—are either vague or can be explained away as an effect of fossilization. In *Cyathodium* the dorsal pores are, as far as I could discover, surprisingly few; normally somewhat elongated (though nearly round sometimes in *C. cavernarum*) and regularly surrounded by one to three rows of small cells with thin walls (Fig. 3A). But in *H. cyathodoides*

the dorsal pores are about twice as numerous as I could find for any species of *Cyathodium*: they are normally round, and the cells around them, though indistinct, do not seem to be much specialised. Moreover, some (but not all) species of *Cyathodium* have pores in the ventral epidermis: nothing like this was seen in *H. cyathodoides*. Another point is that the rhizoids in *Cyathodium* are twice to three times as numerous as in *H. cyathodoides*, and are 2 mm. long or more—thus much longer than any seen in *H. cyathodoides*. It may be also that the rows of cells seen in *H. cyathodoides* are more regular than pronounced than is normal in *Cyathodium*.

(c) *Comparison with certain other pre-Tertiary Liverworts.* The fossil liverworts have been discussed by Walton (1925, 1928) and, more recently, by Harris (1942), Steere (1946) and Lundblad (1954, 1955). The Tertiary ones look very like living genera, and I leave them aside. Of the pre-Tertiary fossils there are eight which require individual attention now; six because they have structures suggesting an air-chamber system within the thallus, and two because they come from a flora containing *Dicroidium*.

The plants that may have an air-chamber system in the thallus are these:

- (i) *Ricciopsis florinii* Lundblad (1954). This plant shows a markedly rosette habit, with very crowded segments, each showing a distinct dorsal furrow. Its rhizoids arise from all over the thallus, especially from the margins, and are 1–2 mm. long. Some are tuberculate, others smooth walled, while yet others show evidence of cross walls and branching. Ventral scales were not observed. The thallus is certainly thick but its internal structure is obscure. At least some of the thallus cells are more or less isodiametric, not elongated.
- (ii) *Ricciopsis scanica* Lundblad (1954) also has a rosette habit, and dorsally grooved segments, but the segments are less crowded than in *R. florinii*. Ventral scales and rhizoids were not observed. The thallus wing is at least two cells thick, the cells forming curving rows from midrib to margin. Internal ribs (whose exact nature is left open) are present, arching out to the margin, and about 0.2 mm. apart. These ribs do not anastomose, but sometimes fork near the margin. Both species of *Ricciopsis* are from the Lower Liassic of Scania, Sweden.
- (iii) *Marchantites hallei* Lundblad (1955) is a large plant, up to 6 mm. wide, and shows well-marked ovate ventral scales along the whole thallus length. The scales, and also the rhizoids, are borne upon thickenings of the thallus that curve out to the margin. The rhizoids are of two sorts, clear and with dark

contents. Air pores are numerous and are believed to be cone or barrel-shaped, and in the figures appear to be elevated. *M. hallei* come from the Lower Cretaceous of Patagonia.

- (iv) *Marchanteolitus porosus* Lundblad (1954) consists of some rather small fragments of a thallus showing elevated air pores sur-

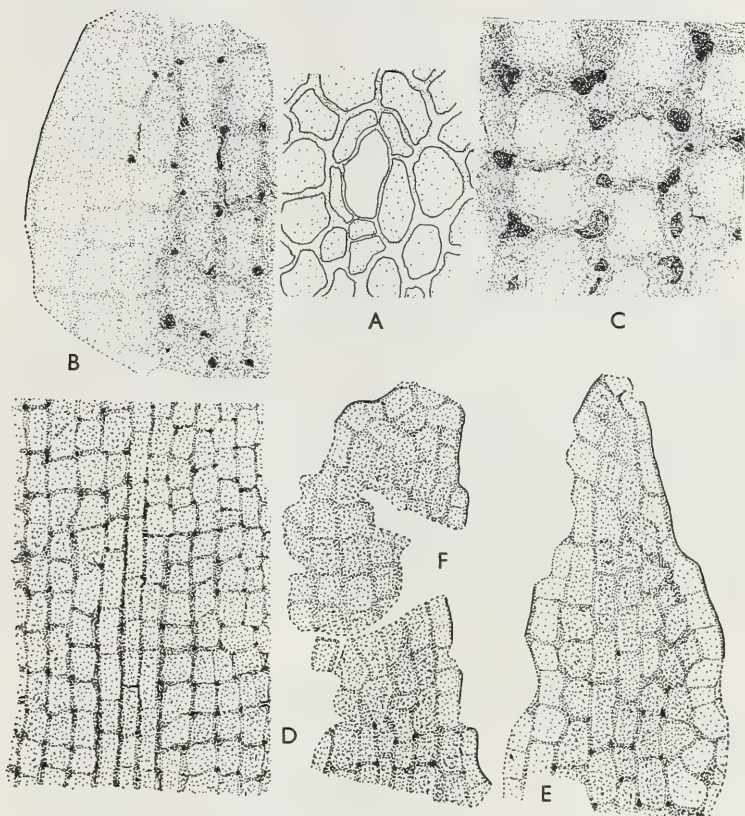


FIG. 3. *Cyathodium aureonitens*, A; *Muscites guescelini*, B-F.

- A. A dorsal pore and surrounding cells (cf. Fig. 1 J.) $\times 160$.
 B. Part of the margin of a leaf, showing square marginal cells, and (at top) their mode of formation, and elongated central cells of thicker substance. $\times 316$.
 C. Cells from an oblong leaf, showing papillae at the corners of the cells, over the cell walls. $\times 316$.
 D. Cells from a leaf, showing the apex of a strip of elongated cells. $\times 176$.
 E. A leaf apex (nearly complete, as interpreted), showing formation of the cell rows and of the margin of square cells. $\times 176$.
 F. A further leaf apex, broken off a little below that shown in Fig. 3 E., but showing similar formation of cell rows and square cells at leaf margin. $\times 176$.

rounded by several rows of apparently modified epidermal cells. It is from the Lower Liassic of Scania.

- (v) *Hepaticites wonnacotti* Harris (1942) is a large plant with a thallus up to 12 mm. broad and with rhizoids up to 40 μ wide. Ventral scales were not seen. The internal structure of *H. wonnacotti* is obscure. The surface shows rather numerous bulges that are internal structures and might be the remains of an air-chamber system. There are also internal thickenings of the thallus; these are best seen acroscopically, and do not anastomose, but are sometimes forked (at about 20°) near the margin. Harris tentatively compared these thickenings with the ribs bearing rhizoids and ventral scales found in some Marchantineae.
- (vi) *Hepaticites haiburnensis* nom. mnsr. Harris, differs from *H. cyathodoides* in being considerably larger and in showing prominent ventral scales. Both *H. wonnacotti* and *H. haiburnensis* are from the Middle Jurassic Deltaic Series of Yorkshire.

The two fossils from a *Dicroidium* containing flora come from Victoria and are described by Medwell (1954). One is called *Marchantites erectus* and is not figured. This name, however, is a synonym of *Hepaticites arcuatus* (L. & H.) Harris (1942). The other is named *Thallites* (originally *Marchantites*) *barwoni* (Medwell) Lundblad (1955). This fossil shows no features that place it definitely in the Bryophyta, and appears to be preserved as an impression only. It consists of two dichotomising thalli, about twice as large as *H. cyathodoides*, and forking at a narrower angle (about 20° from the figure). The margins appear to be waved or scalloped.

As will be seen, none of the above plants are very like *H. cyathodoides*; indeed, *H. cyathodoides* stands rather apart from the other fossil liverworts that are known in any detail.

Since the reproductive structures of *H. cyathodoides* are unknown (and I make no assumptions about their form), I prefer to use the non-committal name *Hepaticites* while indicating the most likely similarity in the trivial name. *Cyathodium* used to be placed in the Targioniaceae, but is now removed to a family on its own (Müller 1952, Reimers 1954); the present specimens do not shed any light on the affinities of *Cyathodium*, but they do indicate that Liverworts with a thallus structure like *Cyathodium* have been distinct for a very long time.

MUSCINEAE

Muscites guescelini

This species is represented by fifteen specimens, twelve of which were made into balsam transfers. The material is well preserved but, as with

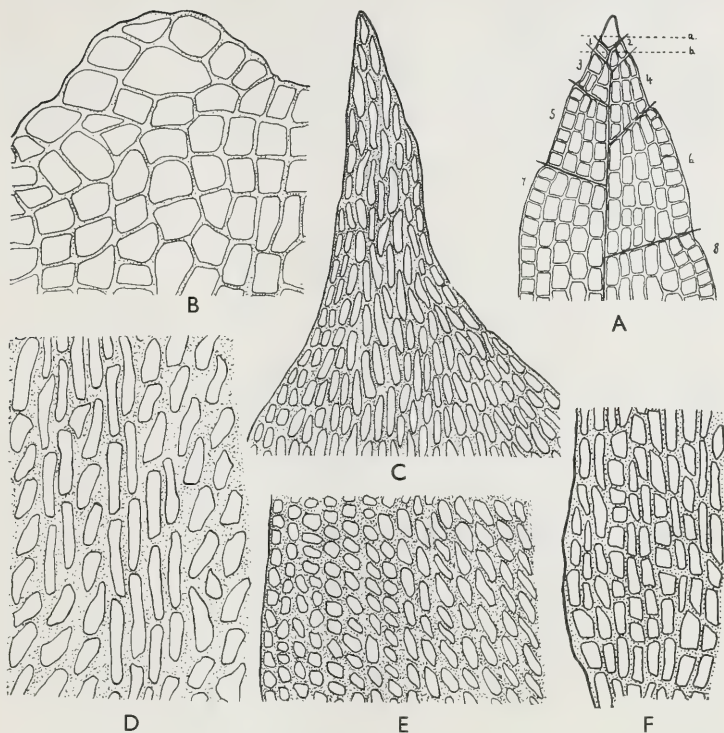


FIG. 4. *Muscites guescelini* (reconstruction), A; *Haplomitrium hookeri*, B; *Leucodon assimilis*, C; *L. giraldii*, D, E; *L. brachypus*, F.

- A. Reconstruction of the leaf apex (somewhat diagrammatic) to show formation of cell rows and margin of square cells from the apical cell. The numbers 1-8 to indicate successive divisions of the apical cell; the lines marked a & b to show the respective levels at which the leaf apices shown in Figs. 3 E, F., are broken off (as interpreted). $\times 118$, approx.
- B. A leaf apex to show the arrangement of the cell rows. Note, further from the apex the transverse arrangement of cell rows becomes obscured, the cells appearing to be set irregularly. $\times 160$.
- C. The leaf apex, showing arrangement of cell rows (cf. Fig. 4 B.), and mode of formation of the square cells at the margin. $\times 176$.
- D. Cells near the leaf base, showing a narrow strip of elongated cells (centre). $\times 475$.
- E. Cells at the margin near the leaf base, showing the inner cells secondarily set in oblique as well as longitudinal rows. $\times 241$.
- F. A leaf showing rectangular cells. $\times 160$.

Hepaticites cyathodoides, some features inevitably remain obscure; so, as in that case, I have made the assumption that the plant was not originally more complicated than it now appears to be.

In order to facilitate the comparisons made in this section, I have examined material of *Naiadita lanceolata* (collected by Professor Harris), and herbarium material of *Haplomitrium hookeri*, most of the genera of the Leucodontaceae, and of various other mosses that showed points that seemed to be valuable for comparison.

The specific name is given after Jocelyn E. S. Townrow, who discovered the first specimen.

***Muscites guescelini* sp. nov.**

(Plate IC—F; Figs. 2B—G, 3B—F, 4A)

DIAGNOSIS: Gametophyte showing sparingly branched stems with an apical tuft of leaves, but leafless below, leafy stems about 1.5 cms. long. Branching apparently equal. Stems about 2 mm. wide and showing elongated epidermal cells about $40\ \mu \times 20\ \mu$. Leaves borne spirally (probably $\frac{3}{8}$) and diverging radially, but at small angle to stem—about 15° , inserted transversely and sheathing for the basal 0.2 mm., margins strongly involute. Free part normally lanceolate, 2 mm. long (extremes 1.25 mm. and 2.5 mm.) and 0.5 mm. wide (extremes 0.25 mm. and 0.75 mm.). Leaf only one cell thick all over, and without a nerve. Leaf cells normally elongated longitudinally, rectangular or hexagonal, $35\ \mu \times 25\ \mu$ (variation $27\ \mu$ and $15\ \mu$). Strips of more elongated cells present, around $50\ \mu \times 20\ \mu$: one to three such strips present, occupying about $\frac{1}{3}$ leaf width at leaf base, and extending $\frac{1}{4}$ — $\frac{1}{3}$ the length of the leaf. Cell walls about $11\ \mu$ thick. All cells set in distinct longitudinal rows, about 20 cell rows per leaf. Cells normally showing thickening or low papilla at corners, papillae up to $10\ \mu$ across. Margin showing one row of roughly square cells apically, three or four rows below, at leaf base roughly square cells occupying about $\frac{1}{4}$ leaf width. Marginal cells about $30\ \mu$ across, cell walls about $8\ \mu$ thick, without papillae. Marginal cells at leaf base sometimes hexagonal, and with papillae. Leaf widening by addition of cell rows to margin, each new row forming a "shoulder" at the leaf edge. Paraphyllia absent. (Rhizoids and reproductive structures unknown.)

DESCRIPTION: The leafy parts of the stems branch at a narrow angle (about 20°), but the leafless stems sometimes show branching nearly at right angles (Plate I E). Most of the stems are now represented by a more or less uniform brown substance, rather obscurely showing the epidermal cells and with indications of several (I do not know how many) cell layers within. A number of specimens show rather darker areas

marginally (Fig. 2G), which probably indicates that there were thickened cells around the periphery of a stem. There was no indication of any central strand of thick cells, which might be expected on compression to show up as a thicker, darker area centrally. Presumably, therefore, any central strand was composed of thin-walled cells only. All the stems are of about the same diameter, so I suppose they were originally round in section, not flattened.

The leaves were certainly borne spirally (Figs. 2B–E) but the phyllotaxis proved hard to determine since all but two rather incomplete specimens were flattened along one bedding plane, and because the leaves were commonly crowded in the apical tuft. The phyllotaxis was not $\frac{1}{3}$, and the value given in the diagnosis $\frac{2}{3}$ fitted the eight specimens that showed a reasonable length of leafy stem better than $\frac{2}{5}$ or $\frac{5}{13}$. It is possible that the phyllotaxis is a more complicated value, but I do not think this is likely. None of the specimens showed any signs of dorsi-ventrality and all, especially those compressed at an angle to the bedding planes, show that the leaves diverged radially. Figs. 2B, C, show the sheathing leaf base and their transverse insertion. There is no evidence preserved suggesting much (if any) torsion of the stem during growth.

The leaf shape varied considerably; the normal form is as given in the diagnosis but, in general, the leaves tended to become more oblong apically, and at one apex (Fig. 2E) oblong not lanceolate leaves are visible. In all cases, however, the leaf was formed of about 20 longitudinal rows of cells, the cells varying in shape, from considerably elongated in the narrow leaves to less elongated and even nearly square in the wider and oblong leaves (Figs. 3B–D). Square cells, away from the margin, were rare. Rectangular cells were commoner than hexagonal cells, and in the hexagonal cells the corners remained angular, not rounded (Plate I F). In the strip or strips of elongated cells the shape was regularly rectangular as it was, too, in the elongated cells at the base of the leaf (Figs. 2F; 3D). I regard the concavity of the leaf at its base as an inevitable consequence of the leaf being wider than the stem. The leaf margin was strongly involute, making the marginal cells difficult to see in many cases.

In none of the specimens could I find any evidence that the leaf was anywhere more than one cell thick.

The longitudinal cell rows are always very distinct, being perhaps, the most prominent feature of the material (Plate IF; Figs. 3D, E). The thickening or papilla at the cell corners was visible nearly everywhere, but most plainly in wide cells. As interpreted, this is not simply a collenchymatous thickening, but, at least where well developed, a distinct protuberance (Fig. 3C for projecting papillae). The marginal

cells were rather often eroded away, but were plain in places (Plate I F; Fig. 3B). As they are paler and have thinner cell walls than the other cells, I suppose they had thinner substance. These cells are square, or if elongated at all, then elongated transversely and so stand out plainly from the rest of the leaf. They become distinct only a very little way behind the leaf apex, while the number of rows of marginal cells increases, passing down the leaf, by division of the row of cells just within the margin (Fig. 3B). At the leaf base the margin is wide, and its cells sometimes papillose, but they still remain paler than the other cells of the leaf (Fig. 2F).

No leaf showed the apex distinctly, but several (Figs. 3E, F) showed the region just behind the apex, and including the base of the apical cell. This cell shows two basicopic faces to which the longitudinal rows of cells can be traced back. At the leaf apex, however, the cell rows are not quite longitudinal, but cross slightly zigzag fashion over a line bisecting the leaf longitudinally (see especially Fig. 3E). Later this zigzag arrangement gives place to strict longitudinal rows. The transverse divisions set in earlier in the marginal cell row than centrally. The marginal cells immediately behind the apex were elongated (Fig. 3E). New cell rows are added (*a*) to the margin; as already noted, at each increase the leaf edge bulges out in a "shoulder" (Figs. 3E, F), and (*b*) apparently irregularly by longitudinal division of a cell situated toward the centre of the leaf.

The shoots were examined for paraphyllia, but nothing resembling paraphyllia was found. It follows, I suppose, that they were absent in this species. Also the stems and the mud left from the transfer process were carefully examined for rhizoids, but, again, none were found. In a few places the cell walls showed slight semicircular hollows, but, as they followed no decipherable pattern, I suspect these hollows are not original features.

DISCUSSION: (*a*) *The form of Muscites guescelini.*

Seven of the specimens appeared mixed up with leaf fragments, twigs and other debris (Plate I D, E) and four others were only small. All, moreover, showed some erosion at the margins and apex. This strongly suggests that this plant is *not* found in its position of growth, but presumably not far from it as most specimens are reasonably complete. It is, thus, not possible to be certain of the habit of *M. guescelini*. However, the different sorts of branching seen in the leafy and leafless stems, and the abundance of leafless stems do suggest that the adult plant had a system of creeping leafless stolons from which leafy branches arose at a wide angle. As the leafy shoots branch more or less equally,

and at a narrow angle, I think it most unlikely that the branching was pinnate.

The form of segmentation of the leaf and the form of the apical cell are of great importance in classifying the material. There are three possibilities.

- (a) That a basal meristem was present, or scattered meristematic cells. The regular arrangement of the cell rows, and the fact that the cell rows can readily be traced back to an apical cell, definitely, I suggest, exclude this possibility.
- (b) That an apical meristematic cell was present, cutting off cells from only one basiscopic face. This situation is seen among the liverworts (see e.g. Schiffner 1924, Campbell 1927, Goebel 1930, Harris 1938), and leads to transverse cell rows in the leaf (see Fig. 4B), though sometimes the cell rows also take on a secondary longitudinal orientation. This is not the arrangement seen in *M. guescelini*.
- (c) That an apical meristematic cell was present, cutting off cells from more than one basiscopic face. This is seen among the mosses (see e.g. Lotsy 1909, Wettstein 1924, Ruhland 1924, Campbell 1927, Goebel 1930), and leads to a leaf showing converging cell rows; that is, the cell rows cross zigzag fashion across a line bisecting the leaf longitudinally. In many mosses the original segments of the apical cell become flattened out by more rapid cell division at the leaf margin, and then the cell rows come to lie longitudinally (Fig. 4C). This is exactly the arrangement seen in *M. guescelini*, and I conclude, therefore, that cells were cut off from more than one basiscopic face of an apical cell that was probably triangular or rhombic in surface views (see reconstruction, Fig. 4A).

(b) *The ascription of M. guescelini to the Muscineae.*

M. guescelini shows a set of characters that today are only found among the Bryophyta, and so I place it here. It also shows, especially in its leaf arrangement and form, and in its cell pattern, a combination of characters that distinguish it sharply from any of the leafy Jungermanniales. The only leafy liverworts that resemble *M. guescelini* at all closely are the Calobryales (see e.g. Gottsche 1843, Goebel 1891, Campbell 1920, Buch 1930, Harris 1938) and the Rhaetic fossil *Naiadita lanceolata* (see Harris 1938, 1939). These two groups have radially symmetrical shoots*, round stems and transversely inserted leaves that are spirally borne.

* The shoot of the Calobryales is sometimes taken to be truly radial, and sometimes as dorsiventral but approaching radial (see Harris 1938). I here regard the shoot as truly radial. If it be taken as essentially dorsiventral, then the comparison with *M. guescelini* is much weakened.

However, both the Calobryales and *Naiadita* show, at least in the young leaf (see Campbell 1929 on *Calobryum*), the cell segmentation that is apparently universal among the liverworts (see above, p. 15)) whereas *M. guescelini* shows, as interpreted, the cell segmentation found among the mosses. This difference I regard as extremely important, for it separates all liverworts from all the mosses, except for three genera. These genera are, *Andrea* (see Kühn 1871, Pottier 1921), *Buxbaumia* and *Diphyscum* (see Goebel 1930), and I am inclined to set them aside as they are all anomalous in other respects.

(c) *Comparison of M. guescelini with the Leucodontaceae.*

As it is interpreted, *M. guescelini* can be matched in a considerable number of features, and in fairly satisfactory detail, with members of the Leucodontaceae, especially with the Leucodontoideae* (see e.g. Okamura 1916, Brotherus 1925, Dixon 1936, Noguchi 1936, 1948), and I am indebted to Dr. E. V. Watson for pointing this out to me. Comparison is close in size, habit, leaf form, cell pattern, shape and ornamentation, and in the absence of paraphyllia. But the comparison is not perfect. There are the following difficulties. (a) The apical tuft of leaves commonly seen in *M. guescelini* is scarcely matched, though some species, e.g. *Leucodon giraldii*, approach closely; (b) the longitudinal cell rows of *M. guescelini* are more regular than, apparently, in any of the Leucodontaceae, though most species of the Leucodontoideae (but not of the Antitrichoideae and Pterogonoideae) are similar (see Figs. 4C, E); (c) the cell dimensions of *M. guescelini* are only just comprehended within the limits of cell dimensions, as far as I can discover them, of the Leucodontaceae; (d) some species of the Leucodontoideae, e.g. *Leucodon brachypus* (see Fig. 4F), have rectangular, rather regular, cells, but most species in this, and the other, sub-families may have cells somewhat differently shaped.

There is also one absolute difference; in the Leucodontaceae the periclinal walls of the marginal cells are thicker than the periclinal walls of the other cells, but in *M. guescelini* the reverse is the case.

However, in addition to the correspondence referred to in general terms above (p. 16), there are two particular similarities. These are (a) the form and mode of development of the square marginal cells, which appear to be identical in *Leucodon* (Fig. 4C), and possibly some other genera, and *M. guescelini*; and (b) the papillae over the cell walls at the corners, which are seen in *Leucodontopsis* and *Pseudocryphaea* (Antitrichoideae), and rarely in *Leucodon*, e.g. sometimes in *L. capensis*.

*The Leucodontaceae are divided into three sub-families (see Reimers 1954), the Leucodontoideae, Antitrichoideae and Pterogonoideae. The chief genus, *Leucodon*, contains about two thirds of the species.

These resemblances are, I think, important, for these characters are only shown by a few other mosses that are otherwise widely different from *M. guescelini* (see pp. 17, 18).

(d) *Comparison of M. guescelini with other mosses.*

A considerable number of mosses resemble *M. guescelini* in one or two points, but differ in more. Many genera have a similar habit, especially in the Families, Bryaceae, Tortulaceae, Dicranaceae, Pottiaceae, Rhacopilaceae, Heterocladiaceae and Amblystegiaceae, but show no other point of approach. Also some genera show papillae over the cell walls at the corners, for example certain of the Bartramiaceae, or *Oxyrrhynchium* (Brachytheciaceae), but, again, these mosses are otherwise quite different from *M. guescelini*. Table I (p. 18) sets out in more detail some of the characters of a number of groups that show similarities in more than one respect to *M. guescelini*, but it will be seen that none come very close.

In conclusion, though the gametophyte of *M. guescelini* is not typical of the gametophytes of the Leucodontaceae, it is much nearer that family than any other. Moreover it shares with the Leucodontaceae two features that are not common among mosses (the form and mode of development of the marginal cells, and papillae over the cell corners) and that are only shown by mosses otherwise very different. Since there is no information about the sporophyte of *M. guescelini*, and in view of its antiquity, I prefer to leave its affinities open and use a non-committal generic name.

GENERAL DISCUSSION.

Species of fossil liverworts are few; there are scarcely twenty fossils known in enough detail for their classification as liverworts to be convincing, though there is a considerably greater number of (mainly) thalloid fossils whose fine structure is unknown, and which it is therefore unrewarding to discuss (see Steere 1946 and Lundblad 1954, 1955). Only two species are known fertile, *Marchantites sezannensis* from the Tertiary of the Paris basin, and *Naiadita lanceolata* from the English Rhaetic. Leaving aside all the Tertiary and later records, the remaining liverworts fall, with very few exceptions, into three groups. The first is a group from the English Coal Measures (Westphalian); the second is a group from the Rhaetic and Liassic, mainly of Sweden and Greenland, but including *Naiadita*; the third is a group from the Middle Jurassic of Yorkshire. Our knowledge, therefore, of the history of the Hepaticae, both as regards morphology and distribution, is markedly deficient. Yet it is peculiar in some respects, for the pre-Tertiary sterile fossils

TABLE I.
Comparison of certain Mosses with *Muscites guescelini*

Plants	Habit	Leaf Form	Cell Pattern			Paraphyllia & Cell Ornamentation
			(a) Margin	(b) Other cells	(c) Strip of elongated cells	
Fontinalaceae	Larger than <i>M. guescelini</i> , otherwise similar	Larger than <i>M. guescelini</i> otherwise similar	No margin of quadrate cells	Cells rhombic, cell walls thinner than <i>M. guescelini</i>	Absent	Cells smooth
Hookeriaceae	Without leafless stolons (except <i>Hookeriopsis</i>)	Leaves scarcely sheathing, apex often blunt, sometimes with nerve	Rarely with margin like <i>M. guescelini</i> (e.g. <i>Crossomitrium</i>)	Cells mostly rhombic with thinner walls than <i>M. guescelini</i>	Absent or very feeble	Cells smooth
Leskeaceae, especially Leskeoideae	Habit similar to <i>M. guescelini</i>	Leaves with nerve	Cell pattern sometimes, but margin rarely like <i>M. guescelini</i>	Distinct from <i>M. guescelini</i>	Strip replaced by nerve	Cells with centrally placed papilla, or smooth
Cryphaceae, especially <i>Bestia</i> and <i>Forsstroemii</i> (Alsiodeae)	Branching pinnate or rub pinnate	Often with nerve	Margin like <i>M. guescelini</i> in <i>Forsstroemia</i> only	Cells set in oblique rows, shape like <i>M. guescelini</i> in <i>Bestia</i>	Strip usually replaced by nerve	Cells smooth, Paraphyllia normally present
Erpodiaceae especially <i>Venturiella</i> and <i>Aulacopilum</i>	Habit similar, but plants only about $\frac{1}{4}$ size of <i>M. guescelini</i>	Nerve present in some species of <i>Aulacopilum</i>	<i>Venturiella</i> with similar margin	Cells not, or scarcely elongated	Absent, replaced by nerve in some species of <i>Aulacopilum</i>	Cells smooth, or papillae centrally placed in some species of <i>Aulacopilum</i>

look like members of living families, or even genera, and not like intermediates between families and genera. In this respect *Hepaticites cyathodoides* is like most other pre-Tertiary liverworts.

The records of fossil mosses are even scantier (see Dixon 1927, Steere 1946). In the Quaternary and later Tertiary many mosses are known, that belong, it appears, to living genera; in the earlier Tertiary there are a few, two or three with fruit, but none known in cellular detail; while from the pre-Tertiary there are (excluding two or three doubtful leaf fragments) only two, both from the Upper Carboniferous (Stephanian) of St. Etienne, and both sterile (see Walton 1928). One, *Muscites polytrichaceus*, is a leafy shoot of moss-like habit but unknown structure, the other, *M. bertrandi*, is a transverse section of an axis showing some moss-like structure, but of unknown habit and leaves. Walton summarises the evidence from these records as follows (p. 714): "there seems little reason to doubt the presence of mosses at least as far back as the Stephanian (Upper Carboniferous) but what their relationships to the living *Musci* were cannot yet be decided". *Muscites guescelini*, on the other hand, because it can be compared fairly closely with a living family, parallels the pre-Tertiary liverworts.

One is bound to ask the question to what extent these, sometimes close, similarities in gametophyte structure can be taken to indicate relationships. For the pre-Tertiary I suggest it is not safe to assume any relationship, though it may exist and might be close. The reasons for this view are as follows:

- (i) There are few fossil bryophytes known and, except *Naiadita*, those that are known are sterile. Often their preservation scarcely allows of reasonable certainty even of their gametophyte structure. They thus shed little or no light on the evolution of the group; so that it is hardly possible to decide whether the fossils that look like living plants are related to them, or are unrelated, merely having evolved a somewhat similar thallus form.
- (ii) Even those fossils that approach nearest to living forms, e.g. *Ricciopsis florinii*, still show definite points of difference that may well be paralleled by differences in their reproductive structures that are as yet unknown. The uncertainty of classifying sterile material remains even in groups, e.g. the conifers, whose fossil history is vastly better known than that of the Bryophyta.
- (iii) The case of *Naiadita*, which is the only fossil bryophyte known fertile and in cellular detail, supports arguments for a conservative approach to this question. This plant proved very

difficult to classify. Had *Naiadita* been known sterile it might have appeared easier to classify; it might have been ascribed to the Calobryales, especially if its rhizoids had also not been preserved.

For reasons such as these, schemes which attempt to utilise such sterile and imperfectly known fossil bryophytes to support a particular theory of evolution are not convincing, because these same fossils could equally well be used to support almost any other theory (see Mahra 1957).

I would also suggest that, for the pre-Tertiary, it is not yet worthwhile multiplying generic names unless they are based (like *Ricciopsis*) on both form and detailed structure. I think there is little, if any, gain, for example, in transferring *Hepaticites glebosus* to a new form genus *Metzgerites* on the strength of its wavy margin and sparingly forked thallus (see Steere 1946).

A feature that proved of the greatest value in discussing *Muscites guescelini*, and was also most valuable in the case of *Naiadita* (see Harris 1938), is the segmentation of the leaf. Indeed, it seems that, for fossil material, this character may be of even greater value than the difference in rhizoid form used to separate the Liverworts and Mosses which is more often mentioned. The cells of the leaf quite often seem to have been better preserved than the rhizoids, and even the rhizoid character has exceptions (see Lundblad 1954), a few liverworts showing septate or branched rhizoids like the Mosses. I imagine that the mode of segmentation may usually be deduced even if the actual apical cell is missing.

A final point worthy of mention, but not to be pressed too far, is that the two species here discussed most closely resemble plants that are now mainly tropical.

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